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THE INFLUENCE OF GRAZING ON LAND SURFACE CLIMATOLOGICAL VARIABLES

(FIFE Project SRB-6)

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Research Accomplishments

1. Empirical Measurements. Net primary productivity and consumption were again measured using the movable exclosure method at four sites (29, 40, 21, 32). Foliage samples have been obtained for nitrogen analyses at these sites.

2. Laboratory analyses. Nitrogen measurements on foliage, root and rhizome samples from 1987 collections were completed.

3. Data analyses. All field and laboratory measurements for 1987 have been encoded and verified. Preliminary analyses comparing grazed and ungrazed prairie for spectral and energy characteristics are either underway or completed. A representative series of SPOT and all TM scenes for 1987 have been rectified and are undergoing enhancement. Interactions with FIS are continuing.

4. Modeling. Procedures and objectives for modeling have been selected and the formal modeling efforts initiated. Dr. Steven Seagle, Syracuse University, is modifying a previously validated grazing model for this project.

Publications

Two manscripts are tentatively in press which contain preliminary results and findings from the FIFE effort. These include:

1. Shapley, T.D., R.A. Ramundo, C.L. Turner, M.I. Dyer and T.R. Seastedt. in press. Effects of burning, mowing and nitrogen fertilizer on chlorophyll, nitrogen, phosphorus and spectral reflectance characteristics of tallgrass prairie. In: Proc. 11th North American Prairie Conf.

2. Seastedt, T.R. and J.M. Briggs. in press. Long-term ecological questions and considerations for taking long-term measurements. Lessons from the LTER and FIFE programs on tallgrass prairie. In: P.G. Risser (ed) International Perspectives on Long-Term Ecological Research. SCOPE, Stockholm, Sweden. These Manuscripts have been appended to this report.

Presentations

Four presentations were made during the funding period that related partially or totally to the FIFE research. In addition to presenting the above manuscripts at the Eleventh North American Prairie Conference in Lincoln Nebraska and at the International LTER workshop in Berchtesgaden, West Germany, the following two presentations were made at the American Institute of Biological Sciences national meeting at Davis, California.

3. Turner, C.L., T.R. Seastedt and M.I. Dyer. Influence of Grazing on Tallgrass Prairie Productivity: Implications to Remote Sensing Measurements.

4. Seastedt, T.R. The FIFE program on the Konza Prairie.

Related Accomplishments:

Seastedt and Briggs have received funding from the KSU Long-Term Ecological Research (LTER) program along with additional support from KSU to purchase a minicomputer with ARC-INFO and ERDAS software. This $97k system will replace the microcomputer/1600 tape drive currently in use, and should greatly enhance our ability to do spatially explicit modeling. This purchase guarantees that all objectives of our three-year effort can be undertaken at Kansas State University. This purchase also represents the initial effort of KSU to become a functional data management facility for a portion of the FIFE data base, should NASA want to terminate support for FIS after 1990.

In Press: Risser, P.G. (ed). International Perspectives of Long-Term Ecological Research. SCOPE, Stockholm.

DRAFT

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Long-Term Ecological Questions and Considerations for Taking Long-Term Measurements: Lessons from the LTER and FIFE Programs on Tallgrass Prairie.

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"We have just enough time left in this century to achieve a major new synthesis and understanding of the Earth System..." (NASA 1988)

Introduction

The earth, with its global problems of overpopulation, over-use and abuse of fossil fuel and nuclear energy, and production of toxic wastes, has often been compared to a sick patient. Usually, the amount of attention given a sick individual is proportional to the severity of the illness. Healthy individuals require but an occasional check-up with measurements focused on long-term health trends. "Illness" is recognized as a significant deviation from the long-term trends. We might take some grim satisfaction in knowing that the continued deterioration of the biosphere mandates measurements such as those underway as part of the Long Term Ecological Research (LTER) program. Long term monitoring does not necessarily imply that we can keep our ecological systems out of intensive care, but this activity represents a minimal activity for responsible individuals and agencies interested in placing current environmental problems into perspective. Long-term measurements are directed at questions involving phenomena not interpretable or perhaps not useful when viewed over short (annual or less) time scales, but are related to the long-term "health" or functioning of the system. Thus, the LTER data provide the context in which short term observational or experimental results can be interpreted (Magnuson, in press).

The rationale for making long-term measurements of biological phenomena is well known in North America (Iker 1983, Likens 1983, Callahan

1984, Strayer et al. 1986, Tilman in press). We believe that the Long-Term Ecological Research (LTER) program can provide a blueprint for current efforts involved in evaluating ecosystem responses to potental changes in energy, water and trace gas dynamics occurring on the earth's surface. Certain LTER studies are especially useful in linking remotely sensed, large-scale measurements to site specific, fine-scale biological phenomena. Such data will provide the necessary empirical information to link global climate models to ecosystem phenomena and in doing so will establish the importance of the biotic system in cause-effect relationships with surface climate. "Focused studies of the interactions between the atmosphere and the biosphere that regulate trace gases can improve both our understanding of terrestrial ecosystems and our ability to predict regional- and global-scale changes in atmospheric chemistry." (Mooney et al. 1987).

This chapter attempts to identify a set of long-term ecological questions that are useful to a national or international network of research sites. While there exists an infinite list of interesting questions that could be addressed with long-term studies, a realistic and goal-oriented list of measurements is presented. The criteria for selecting these questions involved identifying variables that 1) are useful intersite comparisons, 2) are not strongly biased by spatial scaling factors, and 3) can provide the necessary linkages between atmospheric/climatological variables and biological measurements. The list of proposed variables for study was developed from the "core LTER measurements", a guideline used since the inception of the LTER effort (Callahan 1984), from recommendations suggested in Earth System Science (NASA 1988), and from practical experience with the recent NASA-FIFE International Surface Land Climatology Project conducted on the Konza Prairie LTER site (Sellers et al. 1988). While appropriate examples are taken from many terrestrial systems, particular emphasis has been given to questions that have interested researchers studying grasslands. We build on the work of Strayer et al. (1986), "Long-Term Ecological Studies: An Illustrated Account of Their Design, Operation and Importance to Ecology". That important publication provided useful definitions of research productivity, of what constitutes "long-term research" and reasons for the "successes" of previous and existing long-term research efforts. Their findings emphasized that individual scientists and not specific research protocols or experimental designs were largely responsible for successful long-term research efforts. Here, however, we suggest that certain constraints on research designs are important if a goal of the research is to benefit directly a regional or global network.

Finding Appropriate Objects for Long-Term Network Measurements

The five core areas of the LTER include studies of the following topics (Callahan 1984):

1. Spatial and temporal distributions of populations,
2. Patterns and frequency of disturbance,
3. Pattern and control of primary production,
4. Pattern and control of organic matter accumulation, and
5. Patterns of inorganic input and movements through soils.

While excellent research has been done on some or all of these topics at one or more of the LTER sites, the current effort on linking sites in regional or global networks suggests that certain measurements are likely to be more useful than others.

A mechanistic, systems approach suggests that researchers make time-series measurments of atomospheric inputs, the state of the system, and the response variables. Often, this translates to measuring weather, the numbers, kinds and mass of biotic components, and output functions such as changes in the amounts of state variables. The spatial scale at which these parmeters are measured is site-specific. A few sites are fortunate to have "integrated output responses" such as stream chemistry and stream flow data. Other sites can only report net primary and secondary productivity or nutrient fluxes as output responses, often calibrated from microsite measurements. Many of these latter sites therefore focus on community structure phenomena. Using criteria proposed by Rowe (1961), however, we submit that the maximum amount of information per unit of effort can be obtained by studying primary ecological objects (organisms and ecosystems) rather than arbitrary composites of these objects.

The most interesting and useful empirical studies of individual species have been long-term in nature (cf. Iker 1983, Strayer et al. 1986). Studies of within- and between-habitat species diversity with respect to spatial patterns remain of keen interest to many ecologists. Nonetheless, we suggest that individual species, species lists or indicies derived from species lists make poor primary intersite comparison measurements. The species (or population) is not a constant functional unit when viewed either within sites or across environmental gradients. The relevant units to address intersite comparisons must be constants, with units that confer equivalency across sites, and these units must be able to aggregate into meaningful values at different spatial scales. Energy and mass (including elements, trace gases etc.) are the obvious candidates for study. Biologists may still focus on the biota as cause and effect participants in energy and mass transformations, but both the forcing functions and the response variables must employ units common to all sites. Eventually, life history characteristics and physiological responses of the individual species will provide a mechanistic interpretation of site-specific responses. Even then, however, these responses will be governed by spatial patterns not usually measured in population studies (Huston et al. 1988).

All LTER sites have been charged with studying "disturbance" as a core measurement. Our own experience with this topic has suggested two serious problems associated with the concept that may prevent "disturbance ecology" from becoming a major tenet of ecological theory (Evans et al., in press). One problem has been the popularity of the topic, and the inevitable misuse of the term that comes with popularity. "Disturbance" is used simultaneously to describe a system input (e.g., a storm) and system output (e.g. species die-off). Obviously, the latter is the interaction of the system with an input, and is therefore very much a characteristic of the system while the former is uncontrolled by the state of the system. The second problem with disturance theory is that identical inputs can produce very different outputs depending upon the inital state of the system and the scales at which the output is measured. For example, fire adversely affects a number of populations of plants and animals in the tallgrass prairie. Nonetheless, certain species are benefited and periodic fires are required for the perpetuation of the system. Is fire or the absence of fire the disturbance in this system? Can systems lacking stable equalibria be disturbed? System-level properties of resistance and resilience to disturbances can be viewed more logically and mechanistically as consequences of structural and life-history characteristics of biological systems. Our own group found the discussions about species and ecosystem responses to disturbances" to be largely an exercise in after-the-fact descriptive ecology and a topic not conducive to the development of predictive models. A much more productive approach to generic disturbance-type questions involves explicit identification of forcing functions and the responses of the system at specific levels of resolution. In other words, we believe that the LTER core area involving disturbance can be adequately addressed within the context of studies focused on the other core areas. This is certainly true in grasslands and agroecosystems where studies use fire, grazing or tillage practices as experimental manipulations.

The remaining three core areas of the LTER program provide a logical, unified focus for regional and global networks. These core areas employ units that are constants and provide the direct links between biotic and atmospheric processes. A combination of relatively new, spatially explicit measurements, in conjunction with traditional methodologies, will allow ecologists to study biotia-climate interactions while concurrently focusing on questions of local interest.

Primary Productivity

Forested sites have considerable potential to demonstrate the linkages among net primary productivity, trace gases and climatic changes. Dendrochronology studies have used annual woody growth increments to recontruct recent past climates. Other studies have combined paleobotany, records of lake ash deposition, and dendrochonology to reconstruct forest species composition, fire frequency and growth relationships. Clark (1988) demonstrated the relationship between climate and fire frequency which, together, shaped the species composition and productivity of the north temperate forests. Of particular interest has been the work of LaMarche et al. (1984) which suggests that subalpine forests in western North America began to alter their growth patterns with respect to climatic variables sometime in the 1960s. Those authors suggested CO_2 enrichment as a possible factor. Anthropogenic sources of nutrients in bulk precipitation could, perhaps, be an alternative hypothesis. Regardless, the measurement of woody growth and therefore a record of the past productivity is possible at many sites and is a reasonable, partial index of aboveground net primary productivity. Such data are particularly desirable since 1) sampling can be accomplished at a very infrequent, year-to-decades basis, 2) large sample sizes can be obtained and potentially interacting variables (soils, species, etc.) can be evaluated, and 3) the samples can be easily archived so that future analyses or reanalysis of the same, original data set are possible. To complete the story of aboveground productivity, foliage production should be measured. Litterfall or needle production measurements and procedures are common, but should be supplemented, if possible, with satellite derived digital images. These images can provide a spatial perspective not possible with microplot measurements, and the types and uses of currently available satellite images are discussed below.

Retrospective analyses of grassland productivity cannot be as easily accomplished as forest studies. Sedimentation rates of glacial lakes, in conjunction with pollen analyses, may provide some useful historical data. Also, carbon isotope studies of sediments, soils (including paleosols) and groundwaters in conjunction with these or other research may also provide an interesting story, particularly with respect to changes in the composition of C_3 and C_4 plants (O'Leary 1988).

More recent retrospective analyses of indices of grassland productivity can also be conducted using the satellite image archives. Researchers and sites should move quickly to secure these images lest useful information be lost by agencies not funded as data archives. A listing of potential data sources (Table 1) indicates the resolution and information available from each type of satellite. Investigators need to be aware of the various trade-offs involved in using these various types of data, and some important considerations are outlined in Sellers et al. (1988). In general, we believe that the high spatial resolution (small pixel size) of the Landsat TM or SPOT satellites is extremely useful in evaluating within-site topoedaphic or experimental (fire or grazing) effects. However, a seasonal time-series of these types of data is expensive or simply unlikely to be obtained due to relatively infrequent overflights in conjunction with moderate to high probabilities of cloud cover. In contrast, the NOAA-AVHRR satellite provides relatively low spatial resolution (large pixel size) but high temporal resolution, such that cross-site, cross-year and seasonal comparisons are possible. The potential for using these images as analogs of regional productivity and for estimating trace gas interactions and energy exchange is just beginning to be developed. Recent improvements of algorithms, particularly those employing the vegetation index (Tucker et al. 1985, Goward et al. 1986) or some combination of the vegetation index in conjunction with thermal measurements (Sellers et al., unpublished results) can demonstrate both seasonal and long-term trends in plant biomass and plant vigor. We expect that the more sophisticated, high resolution imaging spectrometers scheduled for space orbit in the near future will provide much more useful data for measuring both biomass and plant productivity at moderate scales. This enhancement begins with the anticipated 1991 launch of Landsat 6 with the Enhanced Thematic Mapper (ETM) on board. Eight bands of spectral information are planned, four in the visible (one being a 15 m pixel panchromatic), two in the near-infrared and two in thermal portions of the spectrum. This system is reported to be very sensitive to surface temperature changes and should therefore be very useful in relating vegetation dynamics with energy flux. Subsequent satellite equipment scheduled for the EOS program will make considerable advancements in the spectral resolution of these digital images. These standard products could also be supplemented with aerial photography, including standard panchromatic, color and color IR images. Photographic records are providing useful for a variety of retrospective analyses.

The Interaction between Productivity and Surface Climate

A conceptual model developed by Shugart (Figure 1) suggests how we might think about the relationship of LTER measurements to studies involved in trace gas fluxes. The latter measurements are, by necessity, made on a scale that detects strong diurnal and seasonal fluctuations. In contrast, LTER measurments have a much coarser temporal scale. However, as suggested by the model, these long-term ecological processes function as constraints on short-term physiological processes, and therefore mediate the response of vegetation to climate. Here, we present an example of this phenomenon to emphasize the need to recognize that changes in ecological constraints such as fire frequency, herbivory or nutrient availability may temporarily overshadow direct changes in temperature or rainfall.

Our data on temperate grassland plant productivity demonstrate a strong relationship between the type of management treatment and productivity (Figure 2). The tallgrass prairie requires periodic fires to maintain its species composition and productivity (e.g. Knapp and Seastedt 1986). In average or wet years, annual burning in late spring benefits the C_4 grasses. However, some but not all drier than average years result in more productivity by the combination of C_4 and C_3 grasses, forbs and woody species found in the unburned prairie. Following a fire, the blackened soil surface of burned prairie is exposed to direct solar radiation and converts much of this energy into sensible heat absorbed by the soil (Figure 3). However, by midsummer, the re-establishment of the canopy, in conjunction in greater rates of evapotranspiration, results in a cooler soil surface. This pattern is reversed at the 10 cm depth, where the drier soils on the burned sites lack the thermal enertia of generally moister, litter-covered soils of the unburned sites. The greater rates of evaporation coupled, perhaps, with higher rates of reflected infrared radiation keep burned areas cooler in midsummer than unburned areas (Figure 4). This thermal (channel 6) Landsat TM image shows that burned watersheds are, on average, several degrees cooler than adjacent unburned areas (Figure 5, see also Asrar et al. 1988). These data demonstrate that the ecological constraints operating on the vegetation (here, a spring fire) influence both the hydrologic and energy budget. These changes are detectable at both a micro- and macro-scale level. Obviously, a change in the fire frequency of relatively large tracts of grassland could have an impact on the regional climate.

Grazing by cattle also had a measureable affect on sensible heat as measured by the TM image (Figures 4 & 5). Grazed areas were cooler in August, presumably because the grazed vegetation was physiologically more active than a similar amount of ungrazed vegetation and was transpiring relatively greater volumes of water. Consumers affect both the amounts and physiology of the vegetation and thereby can greatly alter vegetation-climate interactions, particularly in grasslands. Investigators should also be aware that interactions between energy and nutrients may affect consumers such that consumers become important transient controlling factors on net primary productivity (White 1984). These controls can operate directly via consumption of plant parts or indirectly, by controlling plant species composition (Schowalter 1981). Thus, knowledge of consumer populations may contribute to an understanding of vegetation-climate interactions. This observation also has particular relevance in agroecosystems, where biotic mechanisms of consumer regulation have been severely altered.

Nutrients

Virtually all LTER sites measure nutrient inputs, standing crops and outputs. The input data may be restricted to analyses of wetfall, often associated with the National Atmospheric Deposition Program (NADP). This measurement is often inadequate because dryfall deposition or deposition associated with dew can be considerable (e.g. Lindberg et al. 1986). Most sites obtain pH measurements in conjunction with the inputs of nitrate, ammonia, sulfate and the major cations. Inventories of the standing crops of the major elements in vegetation was initiated at many sites during the International Biological Program. Hopefully, such data have been archived for future analyses or as baselines for future comparisons. Our site archives plant and soil samples along with the numerical data. To our knowledge, no LTER site has engaged in long-term monitoring net inputs or outputs of trace gases (CO_2, NO_x, NH_3, HS, or SO_2). However, with the advent of large path-length infrared spectroscopy (Gosz et al. 1988), and procedures to estimate fluxes, this deficiency should be resolved at a few sites at least. Moreover, as mentioned above, the trace gas fluxes are tied to diurnal phenomena occurring under the "constraints" of the ecological processes being studied by the LTER. Empirical results and modeling efforts currently underway as part of FIFE (First ISLSCP Field Experiment) should be able to tell us the relationships and sensitivity of measurements such as productivity to short term and seasonal estimates of gas flux.

Terrestrial temperate and boreal systems tend to exhibit strong nitrogen limitations while tropical systems appear to be often phosphorus limited. Nutrients become constraints on plant growth during periods when energy or water is not limiting, i.e., under conditions otherwise favorable for plant growth (Schimel et al. in review). The nutrient capital of the vegetation itself as well as the available soil reserves may regulate productivity at a particular point in time. An obvious question of interest to those involved with climatic change questions is the extent that nutrient limitations may affect vegetation responses (e.g. Tissue and Oechel 1987). If plant growth is nutrient as opposed to energy limited, then carbon dioxide enrichment and/or increased temperatures should not affect productivity to the extent that would occur without concurrent limitation by nutrients. In tallgrass prairie, an improved energy environment (created by fire) results in a higher nitrogen use efficiency (NUE) of the vegetation (Ojima 1987). With this greater production, however, comes increased detritus build up and nutrient immobilization. In several biomes, including the taiga (van Cleve et al. 1983) and tallgrass prairie (Knapp and Seastedt 1986), plant litter has a direct negative physical effect on energy availability to plants. Detritus production could therefore affect productivity both by affecting usable energy inputs and by influencing nutrient availability. Seasonal shifts in energy, nutrient and water limitations, in conjunction with negative feedbacks resulting from biomass production prevent the system from maximizing its production response. Indices of nutrient availability therefore need to be studied.

Agroecosystems have additional nutrient inputs and outputs not found or not important in natural systems. Nutrient supplements from fertilizers and outputs in the form of harvested plant parts tend to create an artificially dynamic system. Areas employing irrigation also have potential additional exports of trace gases or leaching losses, and certain agricultural practices are probably having a large effect on trace gas dynamics (Mooney et al. 1987). A detailed accounting of these nutrients is warranted given the progressive enrichment of groundwaters with undesirable organics and nitrates. Moreover, the tillage of the soil, the artificial, excessive harvesting of plant nutrients, in conjunction with applications of fertilizers, have created unique situations of nutrient limitation, soil acidification and aluminum toxicity problems for agricultural systems (Adams 1984). Indeed, many sites have been so totally altered by intensive agricultural practices that moderate changes in temperature, rainfall, rainfall chemistry or rainfall pH would appear of secondary consideration relative to the direct human manipulations. Agricultural regions are so vast, however, that their impacts on atmospheric and groundwater chemistry need to be documented. In these systems the "ecological constraints" are the crop and tillage manipulations. These, like fire and grazing in the prairie, control the system interactions and responses to climatic inputs.

Measurement of nutrient outputs from ecosystems has proved to be an extremely relevant and useful long-term index of integrated system behavior. Likens and Bormann (1977), Bormann and Likens (1979) and Likens (1983) have provided ample examples of these measurements. Their work on stream pH and stream nutrient responses to various anthropogenic manipulations comprises some of the most important ecological research of this century. Stream chemical analyses have provided a measurement of the integrated ecosystem response to changes in atmospheric inputs or changes induced by within-system manipulations. In similar fashion, the new generation of remote sensing equipment scheduled for earth orbit within the next 10 years should provide equivalent information for terrestial systems. Multispectral scanner, high-resolution sensors will provide a spatially explicit measurement of the integrated landscape response to changes in atmospheric inputs and landscape manipulations. Certain chemical properties of vegetation including water status and nitrogen content can already be measured to some extent with current satellite data

(Rock et al. 1986, Waring et al. 1986).

Organic Matter

Plant detritus and soil organic matter provide the major reservoir of nutrients in most terrestrial ecosystems. This storage component provides the "resistence" of the system to changes caused by the destruction of the vegetation. The tropics-to-taiga gradient in organic matter is an example of the interaction between net primary productivity, decomposers and climate (Swift et al. 1979). Any brief interpretation of this pattern is an oversimplification. Nonetheless, plants appear to have dealt better with climatic restraints than have the decomposers. In the United States the east-to-west gradient in soil organic matter observed across the prairie is largely controlled by moisture (Jenny 1930). Prediction of changes in the organic reservoir therefore potentially depends upon the interaction of temperature and moisture, and the net effects that these variables have on production and decomposition (Hunt et al. 1988). Thus, if we predict warmer and drier conditions for the North American tallgrass prairie, we would predict the system to shift towards that observed further west. This senario suggests reduced productivity, with an eventual reduction in soil organic matter. One would therefore project relatively enhanced levels of decomposition and mineralization until a new equalibrium between production and decay develops. We would therefore predict an annual net CO_2 release and enhanced nutrient losses via atmospheric or groundwater exports. Soil organic matter measurements tend to be rather insensitive to short-term manipulations of productivity and decomposition, but should be useful monitors of long-term changes (Jenny 1980, Ojima 1987, Ojima et al. in press). Moreover, such data are generally available on a regional basis, and have been modeled very successfully using climate and management constraints as forcing functions

(Parton et al. 1987a, 1987b).

Investigators need to recognize that edaphic factors and climatic variables may produce interaction effects that add to the complexity of regional patterns. A recent example is found in Sala et al. (1988). That study found that sites with certain soil types were relatively more productive under below-average rangefall, while other soil types were relatively more productive under average or above-average rainfall. Such factors must be known if intersite data are to be used in regional predictive models, and the relevance of these findings to models linking ecosystems to global climatic models should be particularly obvious.

Scaling Considerations

The above discussion argues that measurements of factors controlling net primary productivity, nutrient cycling process and organic matter dynamics are likely to be the most useful and relevant contributions of LTER studies to a larger network system. The problem remains, however, as to how to integrate point measurements so that these data can be used as useful estimates of regional dynamics. Among the more obvious problems are dealing with spatial and temporal variability and relating site measurements and site-specific phenomena (species, edaphic factors) to regional averages. The problems of scaling are nothing new; the optimal plot size remains subjective (Wiegert 1962). A large literature on scaling is developing (e.g. Allen et al. 1984, Urban et al. 1987). By far, the most productive approach we have seen involves the use of explicit spatial models to aggregate ecosystem processes (e.g. Huston et al. 1988). Successful large scale regional models of net primary production, nutrient cycling and organic matter dynamics have to date employed a coarser approach based on the ecological constraints of climate and soils (Parton et al. 1987a, 1987b). However, plans are underway to interface the fine-scale, spatially explicit models as inputs to the larger-scaled models (Shugart, this volume). We believe that a minimum of a two-step approach (1. organismic to ecosystem process level phenomena and 2. ecosystem process level phenomena to GCMs) will be required.

Inputs required for global scale models may require large spatial resolution but fine temporal resolution. As discussed above, such data will likely use satellite data and algorithms developed from FIFE-type projects (Sellers et al. 1988). Our own work with that project has convinced us that certain characteristics measured at small plot scales can be directly related to larger scale measurements (e.g. Figures 2-4). These measurements can be scaled up to function in input-output relationships with GCMs. However, large errors will be introduced if the "ecological constraints" (i.e. land management) contributions are not included. In our region, changes in the "ecological constraints" to net primary productivity, i.e., fire, fire history or grazing in prairie or changes in cropping and tillage practices in agroecosystems, will alter these algorithms.

The LTER sites must also serve as indices of system response to changes in atmospheric inputs. The long-term acid rain studies of Hubbard Brook (Likens 1983) are typical examples of this function. Such information may be relatively easier to address for some systems and for some variables over others. Consider the problems associated with measuring export of nutrients from two watersheds (Figure 6). In the Dismal River system, a few baseflow samples accompanied by a storm-event sampler should produce a very accurate measure of export. The lack of inherent variability and high degree of predictablility in flow from this sandhills prairie makes detection of patterns and trends a potentially easy task. In contrast, the Blue Beaver Creek system in Oklahoma exhibits extreme variability and little predictability. Stream discharge appears to be largely controlled by surface runoff in this mixed-grass drainage. The ability to show some statistically significant change in export in this system as a result of changes in land management or climatological inputs would be difficult if not impossible for studies shorter than a decade in duration. This high variability in stream flow is correlated with high variability in annual foliage productivity of North American grasslands (Figure 7). This illustration, taken from Sala et al. (1988) was created by looking at differences in foliage production between good and bad years, divided by the average foliage production. The graph indicates that the sandhills of Nebraska is a relatively more stable environment than the western plains of Oklahoma. This variability, itself, can become a long-term measurement, and an analysis of regional variability such as that conducted by Sala et al. (1988) should identify sites that have intrinsicly lower variability. For studies interested in evaluating directional changes, low variability/high predictability sites and variables appear to be a desirable characteristic. Properties of ecosystems such as net primary productivity are certainly less variable and less sensitive to the vagaries of climate than are the individual species. Moreover, deviations from established relationships between NPP and climate (e.g. LaMarche et al. 1984) would appear to also be useful in correcting for normal yearly variations in climate.

Documentation and Data Base Management

The value of creating permanent plots, adequately documenting procedures, and creating a user-friendly data base cannot be overemphasized. With few exceptions, data bases have not outlived the investigators that collected them (Strayer et al. 1986). Those that have survived have become ecological treasures. Tilman (in press) noted that about 90% of all field studies are three years or shorter in duration. Even these short-term studies, if adequately documented and site referenced, could be subsequently resampled for similar or other ecological questions. We feel that we have lost many thousands of dollars of valuble data because a number of ecological studies with a "short-term focus" were not well documented on our site. Since those projects were terminated, we've come up with a number of questions that could have been addressed if we could only locate the site where the original measurements were obtained. A similar arguement can be made for user-friendly documentation of the data. We've found a variety of new questions for old data sets. These data can be quickly retrieved and reanalyzed, even in the absence of the individual(s) responsible for the original data set. One cannot be serious about measuring decade-to-century level phenomena without making a serious time and financial commitment to documentation. Researchers are referred to Gurtz (1986) and other references in Michener (1986) for excellent guidelines in this area.

Conclusions

The recent Earth System Science Report (NASA 1988), in their recommendations and review of ongoing and proposed research for the IGBP, concluded, "The overwhelming importance of sustained, long-term measurements of global variables emerges clearly from these studies" (pg 137). Here, we contend that a subset of the LTER core measurements, NPP, nutrients and organic matter dynamics, are particularly appropriate for relating vegetation dynamics to surface climatological measurements at a regional or larger scale. Our preliminary results from FIFE suggest that biophysical measurements obtained from small plots, measured under known ecological constraints, will scale up in a fashion conducive the to modeling approaches suggested by Urban et al. (1987). In our region these ecological constraints include the fire and grazing regimes of the grasslands, or the particular management practice imposed on agroecosystems. We do not mean to ignore biodiversity efforts, and emphasize that species-level characteristics are driving the spatially explicit site responses (Huston et al. 1988). Nonetheless, these effects must be translated into biophysical rather than simply biological units to be useful at the intersite level.

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Figure Legends

Figure 1. Conceptual model by H.H. Shugart suggesting the relationships between LTER-type measurements (right side of figure) and those variables strongly influenced by diurnal variations (left side of figure).

Figure 2. Time series of maximum foliage production on annually burned and unburned prairie. Year-to-year climatic fluctuations affect the vegetation response to treatment.

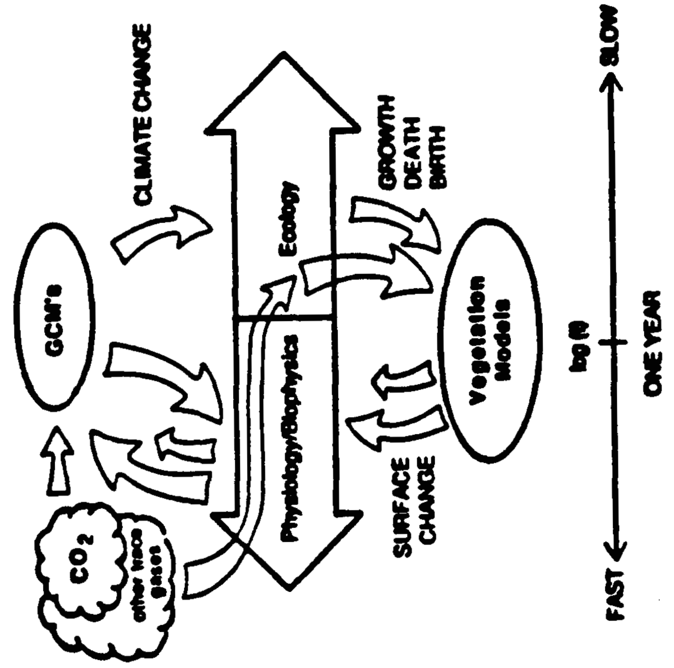
Figure 3. Weekly mean minimum-maximum soil temperatures in summer 1987 for burned (solid lines) and unburned (dashed lines) tallgrass prairie at 2 cm and 10 cm soil depths. Note that temperatures are relatively cooler on the burned site at 2 cm but are relatively warmer at 10 cm.

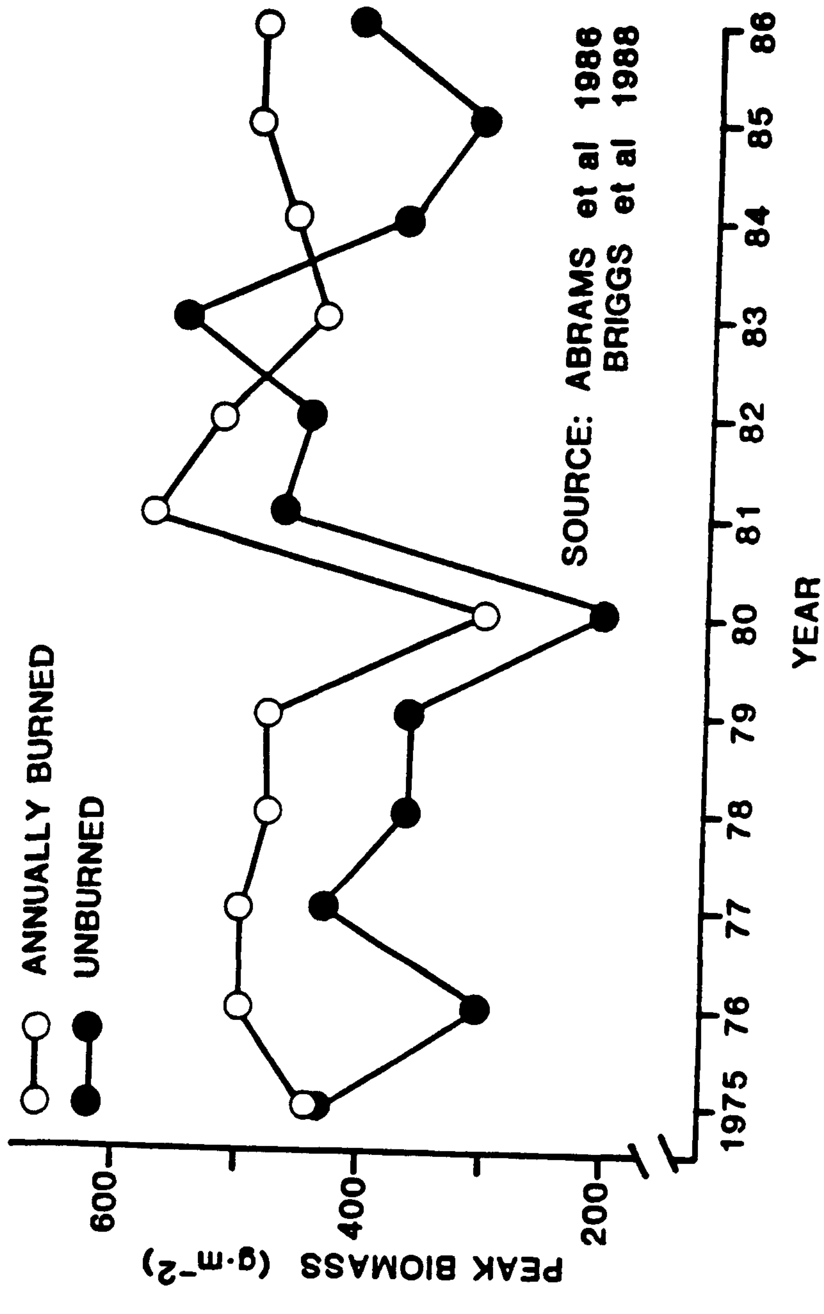
Figure 4. A Landsat TM thermal (channel 6) photo of Konza Prairie Research Natural Area, a site owned by The Nature Conservancy and managed by Kansas State University. Watershed boundaries have been superimposed over the image. Burned watersheds or grazed pastures are distinguishable by the darker pixel values.

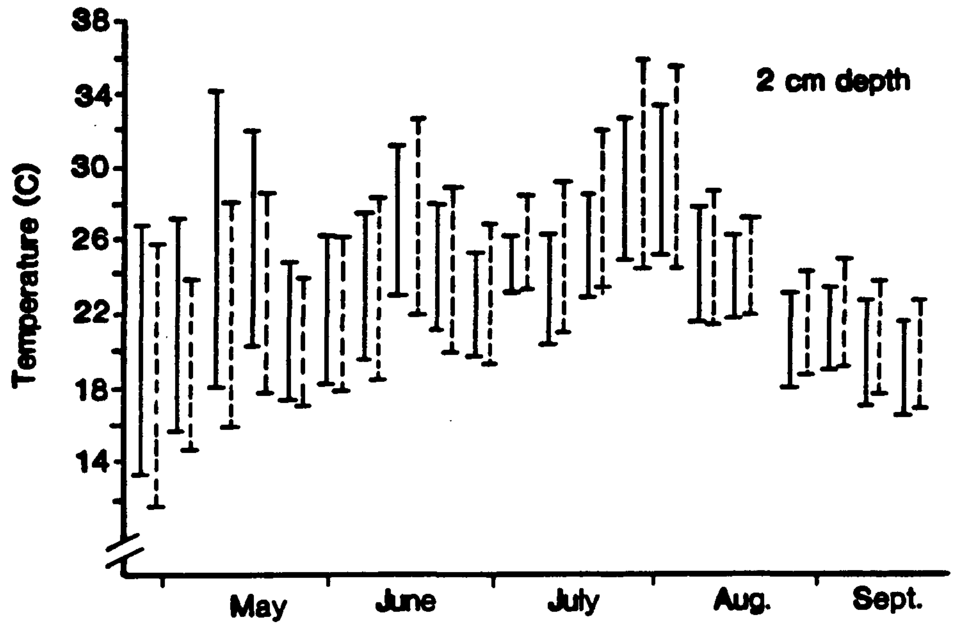
Figure 5. Means and standard deviations of pixel values from Figure 4. All treatments exhibit statistically different values.

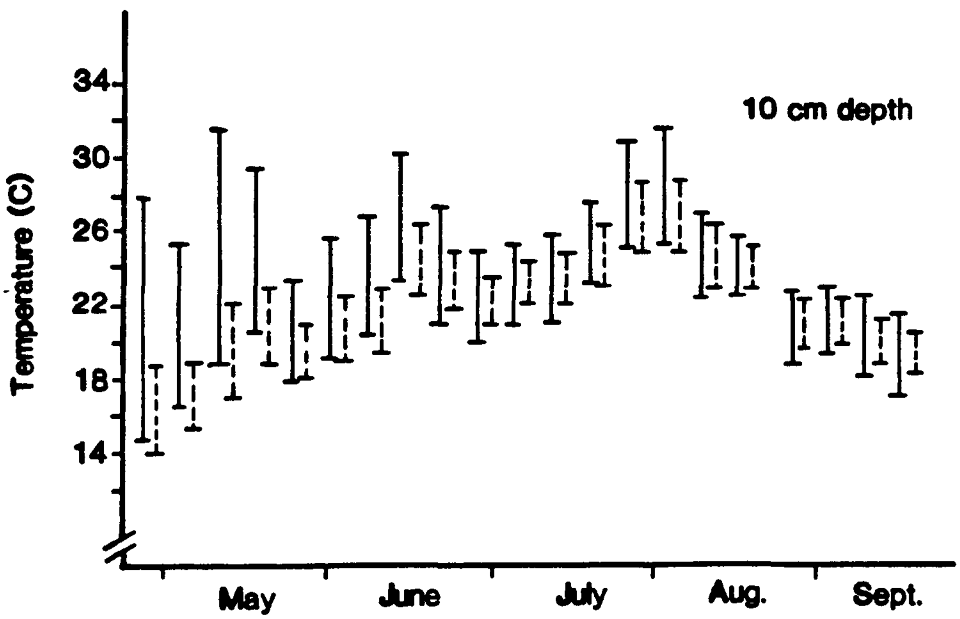
Figure 6. An 18 year record of maximum monthly streamflow from two US Geological Survey Benchmark watersheds.

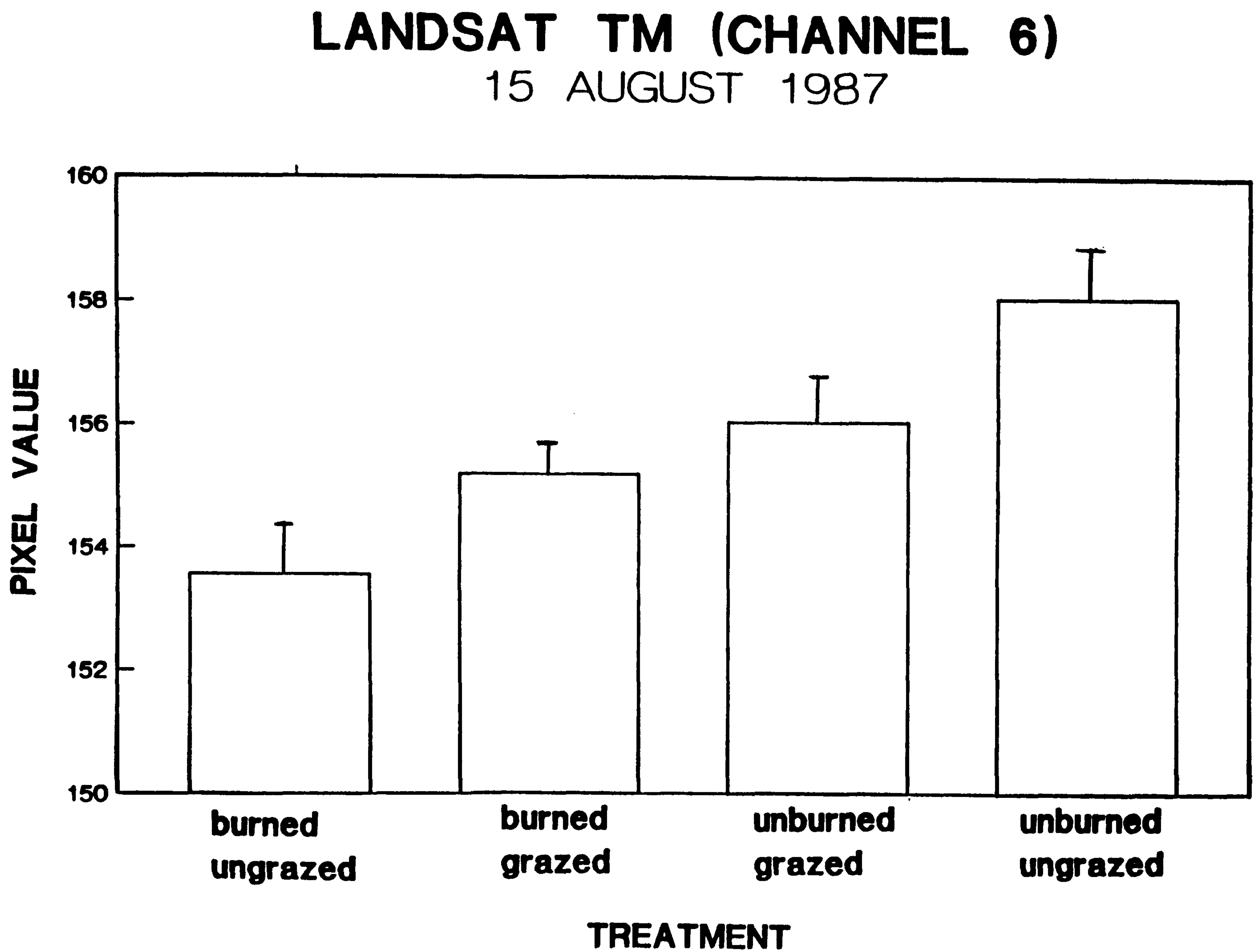
Figure 7. Variation in foliage production in the central U.S (Mean values of good years minus mean values in bad years, divided by the overall mean; Sala et al. 1988).

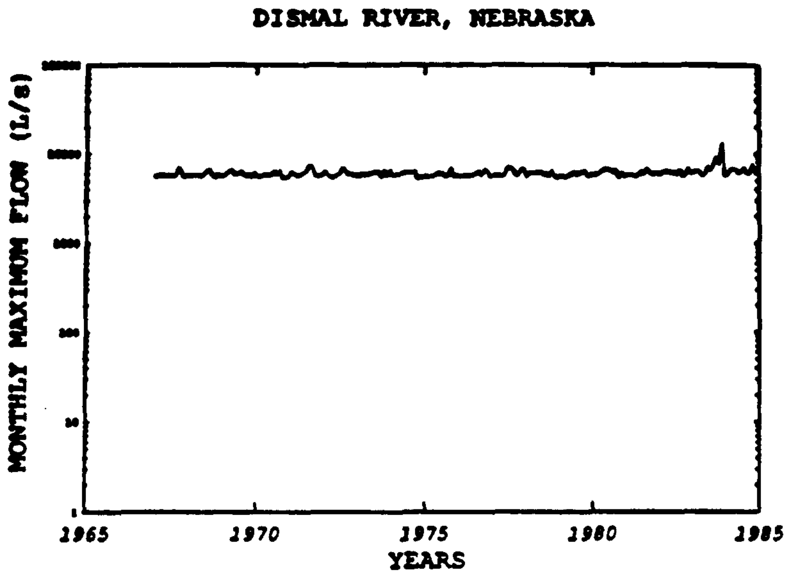

GCM's
CLIMATE CHANGE
CO_2
other trace gases
Ecology
Physiology/Biophysics
GROWTH
DEATH
BIRTH
SURFACE
CHANGE
Vegetation
Models
log (t)
FAST
SLOW
ONE YEAR

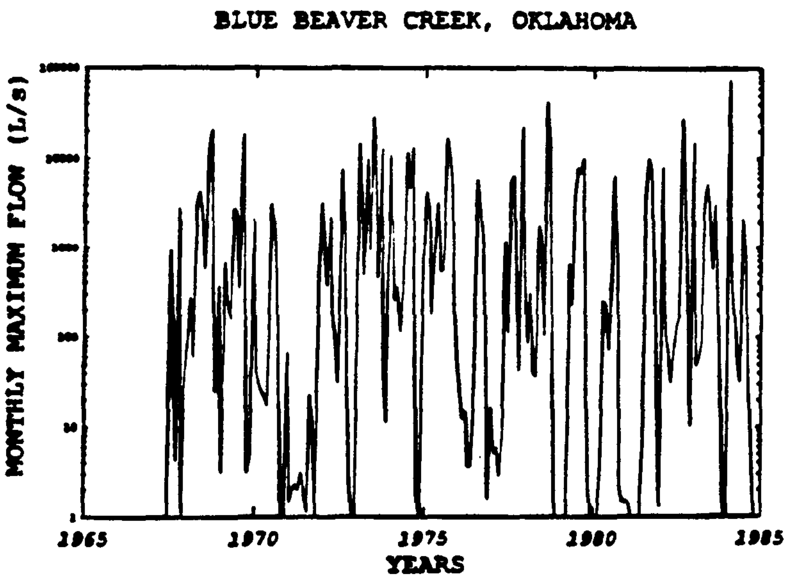

ANNUALLY BURNED
UNBURNED
PEAK BIOMASS (g·m⁻²)
600
400
200
1975
76
77
78
79
80
81
82
83
84
85
86
YEAR
SOURCE: ABRAMS et al 1986
BRIGGS et al 1988


38
34
30
26
22
18
14
Temperature (C)
2 cm depth
May
June
July
Aug.
Sept.

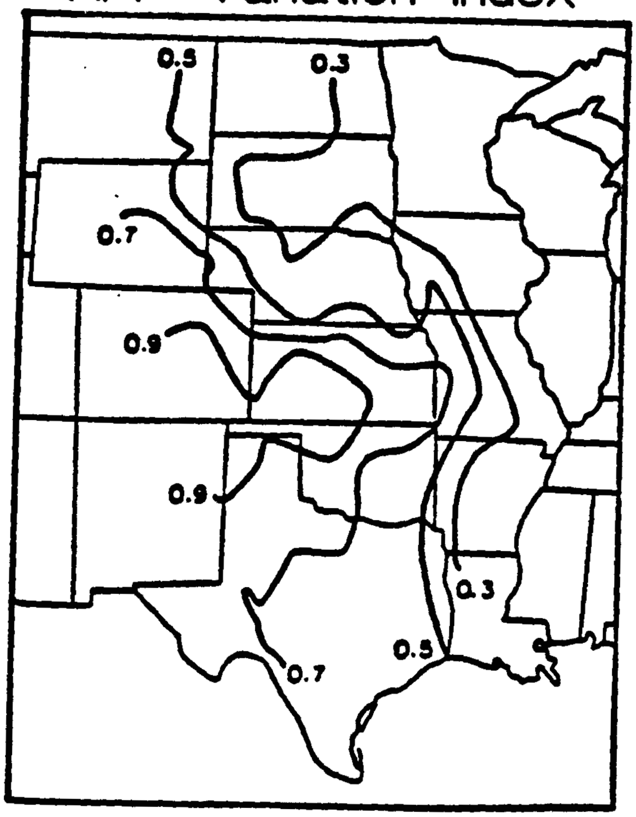

34
30
26
22
18
14
Temperature (C)
10 cm depth
May
June
July
Aug.
Sept.


LANDSAT TM (CHANNEL 6)
15 AUGUST 1987
PIXEL VALUE
160
158
156
154
152
150
burned ungrazed
burned grazed
unburned grazed
unburned ungrazed
TREATMENT


DISMAL RIVER, NEBRASKA
MONTHLY MAXIMUM FLOW (L/s)
1965
1970
1975
1980
1985
YEARS


BLUE BEAVER CREEK, OKLAHOMA
MONTHLY MAXIMUM FLOW (L/s)
1965
1970
1975
1980
1985
YEARS

NPP Variation Index



(Sala et al. 1988)

EFFECTS OF BURNING, MOWING AND NITROGEN FERTILIZER ON CHLOROPHYLL, NITROGEN AND PHOSPHORUS CONTENT OF BIG BLUESTEM (*Andropogon gerardii* VITMAN) AT KONZA PRAIRIE.

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ABSTRACT

The effects of burning, mowing and nitrogen fertilizer addition on the chlorophyll, nitrogen and phosphorus content of big bluestem were measured using a factorial experimental design at Konza Prairie Research Natural Area. While spring burning usually increases foliage production, burning had no effect on mid-season chlorophyll or nitrogen concentrations. Chlorophyll concentrations were significantly increased by fertilizer and mowing treatments. Nitrogen concentrations of foliage were higher on fertilized and mowed plots. Mowing also increased phosphorus concentrations of foliage, but nitrogen fertilizer addition significantly reduced phosphorus concentrations. These results support other research indicating that 1) nitrogen use efficiency (grams biomass produced per gram of foliage nitrogen) is higher on burned prairie, 2) removal of foliage by mowing results in more nutrient-rich regrowth, and 3) the absolute amount of phosphorus available to big bluestem foliage is limited. The dilution of phosphorus caused by nitrogen addition was a consequence of increased productivity on these plots and suggests phosphorus uptake in excess of requirements for maximum growth. The relationships between burning, mowing and nitrogen additions on the spectral reflectance patterns of vegetation indicated that chlorophyll (or nitrogen) concentrations of foliage appeared to more strongly affect indices of greenness and plant vigor than did the amount of plant biomass.

Introduction

A large and growing literature is available on the factors controlling the productivity of tallgrass prairie (Knapp and Seastedt 1986, Ojima 1987, Hulbert 1988). Current scientific emphasis is directed at understanding of spatial patterns of productivity in relation to topography, fire and grazing. There is a growing interest in the use of remote sensing procedures in these efforts (Schimel et al. in review). Spectral reflectance patterns have been used to monitor seasonal patterns of productivity both within and among terrestrial ecosystems (Goward et al. 1985, Asrar et al. 1986). In order for this type of approach to be useful in tallgrass prairie, knowledge of burning, mowing and grazing effects on plant spectral reflectance characteristics must be understood on both on a per unit of foliage and per unit of area of vegetation. Plant physiology and morphology, in conjunction with the absolute amounts of living and dead foliage, will affect the spectral reflectance measurements (Sellers 1985, Waring et al. 1985).

The present study evaluated the effects of burning, mowing and fertilizer additions on the chlorophyll, nitrogen and phosphorus content of the dominant tallgrass species, big bluestem (*Andropogon gerardii* Vit.). These results are then related to the effects of the respective treatments on prairie productivity and the spectral reflectance properties of this vegetation.

Study Site and Methods

Research was conducted on the Konza Prairie Research Natural Area, a site owned by the Nature Conservancy in the Flint Hills region of northeastern Kansas. The study area consisted of 32, 100 m^2 plots that had been 1) annually burned or unburned since 1985, 2) mowed and raked twice per growing season or unmowed since 1985, and 3) fertilized with 10 g/m^2 of nitrogen as NH_4NO_3 or untreated. This 2 x 2 x 2 factorial design resulted in four replicates of 8 specific combinations of burning, mowing and fertilizer additions. Mowing was conducted in late May and in mid July. The species composition of these plots are similar to those reported by Hulbert (1988). Big bluestem was the dominant grass, but Indiangrass (Sorgastrum nutans (L.) Nash) was also abundant. Forbs, including several milkweed species and several goldenrod species, were also common, particularly in unmowed plots.

Samples of big bluestem foliage for chorophyll and nutrient analyses were collected on 3 July 1987 and immediately placed in refrigerated bags and returned to the laboratory. Leaf sheaths were removed prior to measurements. Wet weights of these samples were obtained and samples were then frozen until other analyses were conducted. Quantitative samples for biomass estimates were obtained on 15 July by clipping 0.1 m^2 of vegetation from each plot. Biomass from mowed plots represented regrowth after one mowing while biomass from unmowed plots represented total foliage production.

Methods of both extraction and spectrophotometric analysis of chlorophyll were based on the Delaney technique as used by Knapp and Gilliam (1985). The leaves were taken from the freezer one at a time, thawed by warming gently between the palms, then cut into 1 cm pieces and weighed out on a Mettler balance to 0.01 g. Chlorophyll A, B and beta carotine was then extracted using 85% acetone, sand and $CaCO_3$ in a foil-covered mortar and pestle. The leaves were ground for 1-2 minutes with a Talboy blender. The ground tissue and acetone were poured out into a foil-covered, graduated centrifuge tube and diluted up to 10 ml with acetone. Each sample was centrifuged for 5 minutes and allowed to settle for 1 hour before measured in wavelengths of 750, 663, 644, 452 nm on a Beckmann DB-GT spectrophotometer (Robbelen 1957).

Nitrogen and phosphorus values for foliage samples were obtained by drying and grinding additional foliage, digesting this tissue with a micro-Kjeldahl method, and determining nitrogen and phosphorus colorimetrically on a Technicon Autoanalyzer. Wet and dry weights of leaves were obtained before grinding. The wet-dry ratio of the foliage was later used to convert chlorophyll sample weights for comparison of chlorophyll values with those of similar studies.

Spectral reflectance measurements were concurrently obtained by personnel involved on the NASA-FIFE experiment (FIFE = First ISLSCP Field Experiment, ISLSCP = International Satellite Land Surface Climatology Project). The spectral measurements measure total amount of reflected light at specific wavelengths. Here, an index of "greenness", (Green Vegetation Index, GVI, Kauth and Thomas 1976) based on a linear combination of reflectances of various wavelengths, is used to describe the plots. Another index of plant vigor used to describe the plots, the normalized difference, is a ratio estimator created by subtracting red reflectance from the near-infrared reflectance and dividing this value by the sum of these reflectances (Goward et al. 1985).

Results

An analysis of variance of nitrogen concentrations indicated no interactions among the main treatments of burning, mowing and nitrogen additions. Nitrogen concentrations in foliage of big bluestem were higher in the fertilized plots than in control plots (Figure 1). There also were significantly higher nitrogen concentrations in mowed plots. Spring burning, however, did not significantly affect nitrogen concentrations (Figure 1).

An analysis of variance also indicated no interactions among the main treatment effects for phosphorus concentrations of foliage. Phosphorus increased in mowed plots at about the same ratio as the nitrogen increase (Figure 2). In contrast, phosphorus significantly decreased in plots where nitrogen fertilizer was added (Figure 2).

Fertilization with ammonium nitrate resulted in higher chlorophyll A and total pigment concentrations in big bluestem foliage (Figures 3 and 4). Mowing also significantly increased pigment concentrations while spring burning had no effect. An analysis of variance indicated modest interactions between mowing and fertilizer additions (for chlorophyll A concentrations) and for mowing and burning (for total pigment concentrations). Unmowed, unfertilized vegetation had lower chlorophyll A concentrations than mowed, unfertilized vegetation while concentrations were identical for mowed or unmowed but fertilized vegetation. Burning tended to increase pigment concentrations on unmowed sites but decreased concentrations on mowed sites.

Plant biomass on the various plots was harvested on 15 July (Figure 5). Regrowth after mowing in late may on mowed plots was much greater on fertilized than on unfertilized plots. Overall, these midseason values show a strong mowing and fertilizer effect, and a non-significant effect of spring burning on plant biomass. Indices of plant greenness and plant vigor associated with this biomass are shown in Figures 6 & 7. When these values are compared with plant biomass (Fig. 5), "greenness" appears to be more associated with nitrogen additions than with biomass, per se. An analysis of variance of the reflectance-derived values indicated that all treatments except mowing and all two-way interactions among treatments were statistically significant. In other words, the combinations of mowed and burned plots, mowed and fertilized plots and burned and fertilized plots each produced unique reflectance values. However, the amount of variance attributed to fertilizer addition was much more significant than any other variable or combination of treatments.

Discussion

Midseason chlorophyll concentrations measured here for big bluestem are, on average, somewhat higher than values reported by other investigators (e.g. Bray 1960, Ovington and Lawrence 1967, Old 1969, Knapp and Gilliam 1985). These higher values reported in this study may reflect differences in methodologies rather than actual species differences or differences attributed to site effects. The age of the foliage at the time the chlorophyll measurements were made is important, although Ovington and Lawrence (1967) found little seasonal dynamics in concentrations of total chlorophyll in a Minnesota prairie.

Spring burning did not affect midseason chlorophyll or nitrogen concentrations. While the seasonality of nitrogen content of burned and unburned vegetation may differ markedly (Owensby et al. 1972), the overall amount of nitrogen available to vegetation on burned sites is not markedly different from unburned sites (Ojima 1987). This implies that the increased productivity observed on burned sites in most years corresponds to inceased nitrogen use efficiency by this vegetation. The beneficial effect of burning therefore is attributable to factors other than nutrient availability.

Old (1969) measured the effects of nitrogen addition on mid-season chlorophyll content and reported about a 20% increase in chlorophyll, a relative difference similar to that found in our study (Figure 3). This increase appears to be linearly related to the nitrogen content of this tissue. In contrast, phosphorus concentrations are not related to chlorophyll concentrations. While mowing increases chlorphyll, nitrogen and phosphorus concentrations, addition of ammonium nitrate increases chlorphyll and nitrogen concentrations, but decreases phosphorus content. These data therefore suggest that big bluestem will accumulate phosphorus in concentrations higher than those limiting growth, i.e., the plant exhibits luxury uptake of this element relative to nitrogen and/or other elements.

Our results indicate that "greenness" or plant vigor as measured with the normalized difference procedure is sensitive to both burning and chlorophyll (nitrogen) content of the vegetation. The former treatment, which in our study did not significantly affect nitrogen concentrations, removes standing dead plant materials and litter and thereby changes the reflectance properties of the soil surface. Fertilization and mowing strongly affect nitrogen and chlorophyll concentrations. The reduction in biomass resulting from mowing may negate the positive effect that mowing has on chlorophyll and nitrogen content, such that measurements of greenness after a certain period of regrowth on mowed plots does not show a strong mowing effect. Other studies have suggested that canopy reflectance is sensitive to the physiological status of the plant at the time of measurement (Sellers 1985). Our work tends to support this concept in that plots with reduced biomass but enhanced nitrogen content tend to have equal or greater indices of greenness than unmowed but unfertilized vegetation (Figure 7). These findings have important implications to studies interested in assessing plant productivity or vegetation interactions with the atmosphere by remote sensing methods.

Acknowledgments

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Figure Legends

Figure 1. Nitrogen concentrations of big bluestem foliage. Controls (C), represented by hatched bars, are compared to burned (B) plots, mowed (M) plots, or fertilized (F) plots. Error bars represent one standard error for 16 replicates.

Figure 2. Phosphorus concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

Figure 3. Chlorophyll A concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

Figure 4. Total pigment (chlorophyll A,B and beta carotines) of big bluestem foliage. Symbols are same as those used in Figure 1.

Figure 5. Midseason foliage biomass on burned, mowed and fertilized plots. Hatched bars represent the fertilized plots within each mowing and burning treatements.

Figure 6. Normalized difference, another index of plant vigor, for burned, mowed and fertilized plots. Symbols are the same as those used in Figure 5.

Figure 7. "Greenness" (green vegetation index of Kauth and Thomas, 1976) in relation to burning, mowing and fertilizer treatments. Controls (C), are compared to fertilized plots (F) within each mowing and burning treatment. Bars are one standard error for 8 replicates.

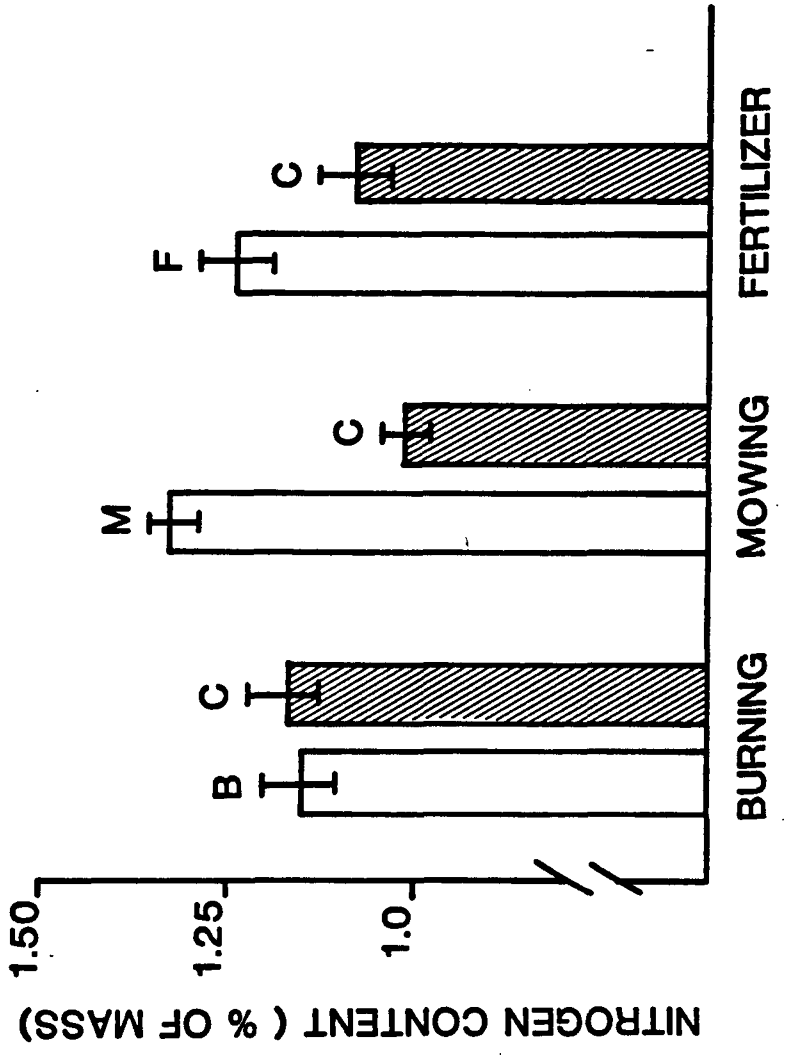
NITROGEN CONTENT (% OF MASS)
1.50
1.25
1.0
B
C
M
C
F
C
BURNING
MOWING
FERTILIZER

Figure 1

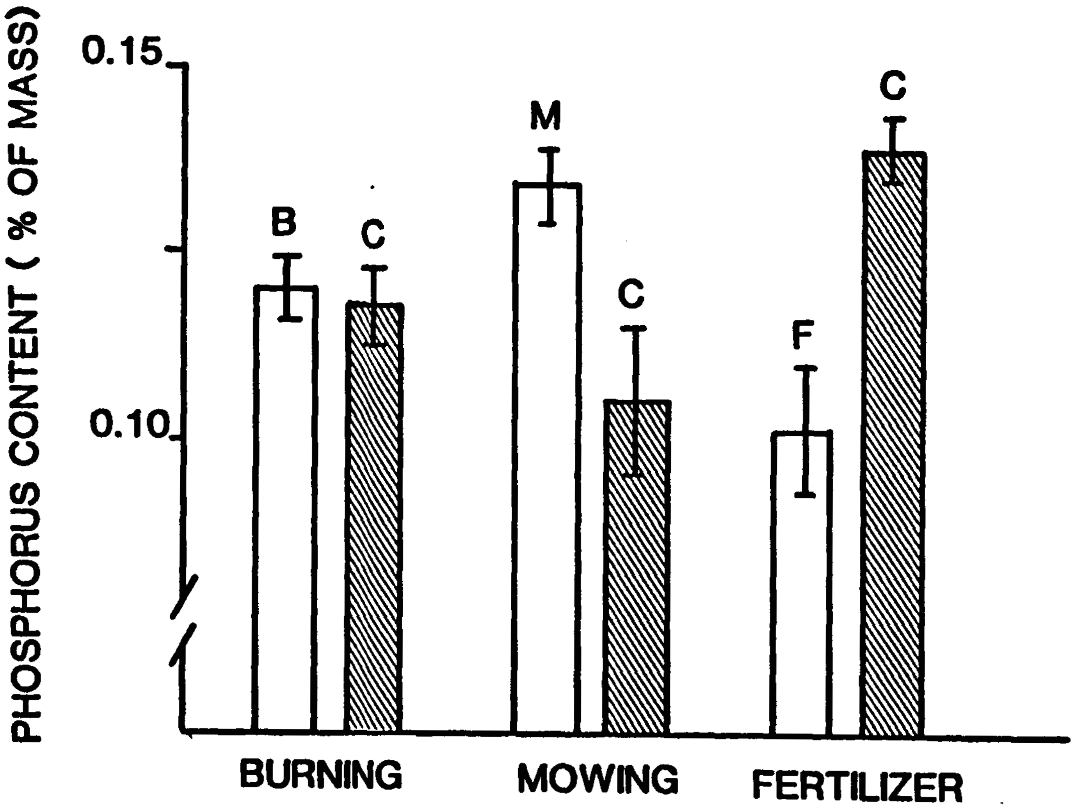
PHOSPHORUS CONTENT (% OF MASS)
0.15
0.10
B
C
M
C
F
C
BURNING
MOWING
FERTILIZER

Figure 2

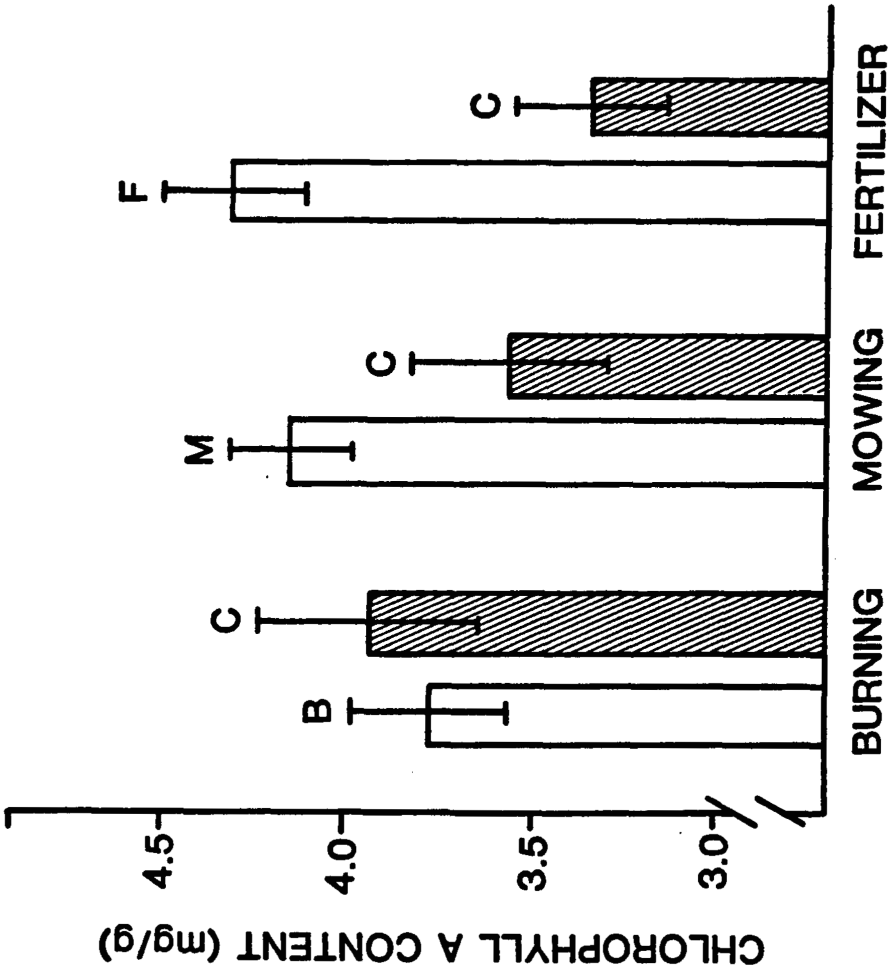
CHLOROPHYLL A CONTENT (mg/g)
4.5
4.0
3.5
3.0
B
C
M
C
F
C
BURNING
MOWING
FERTILIZER

Fig 3

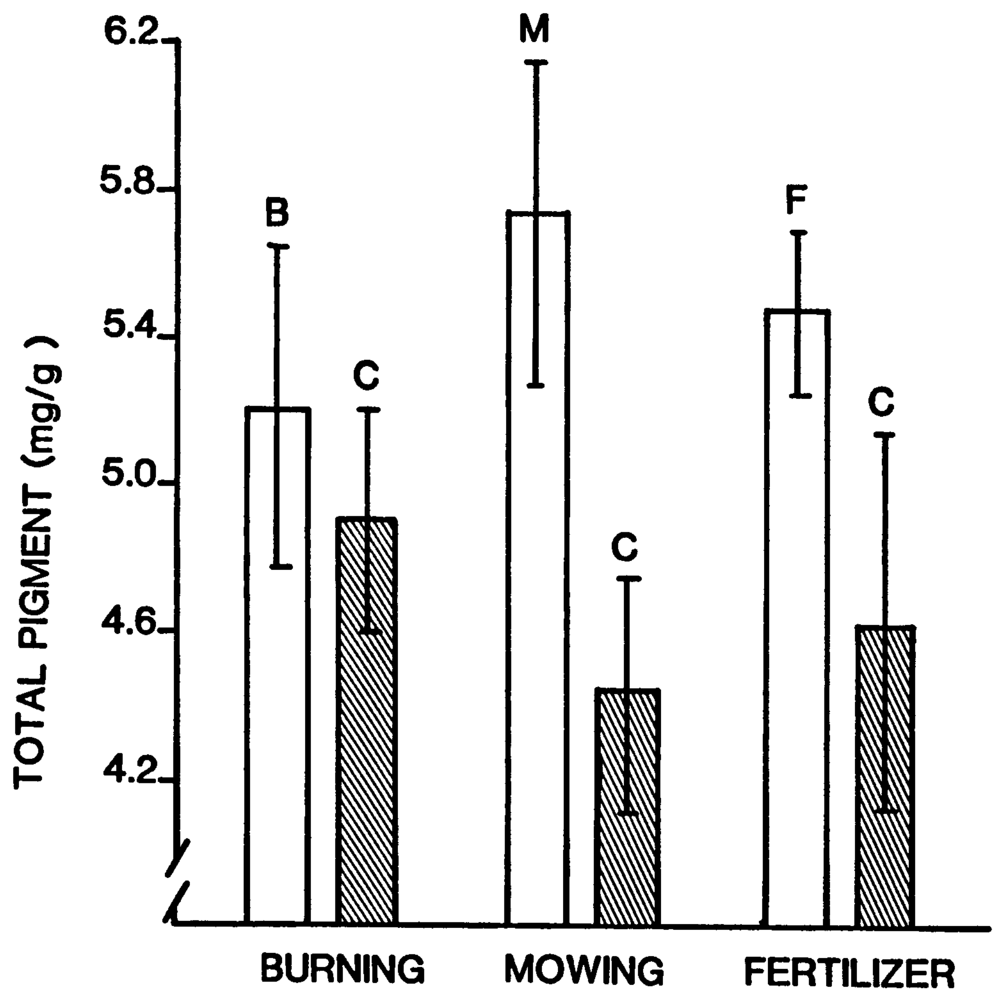
6.2
5.8
5.4
5.0
4.6
4.2
TOTAL PIGMENT (mg/g)
B
C
M
C
F
C
BURNING
MOWING
FERTILIZER

Fig 4

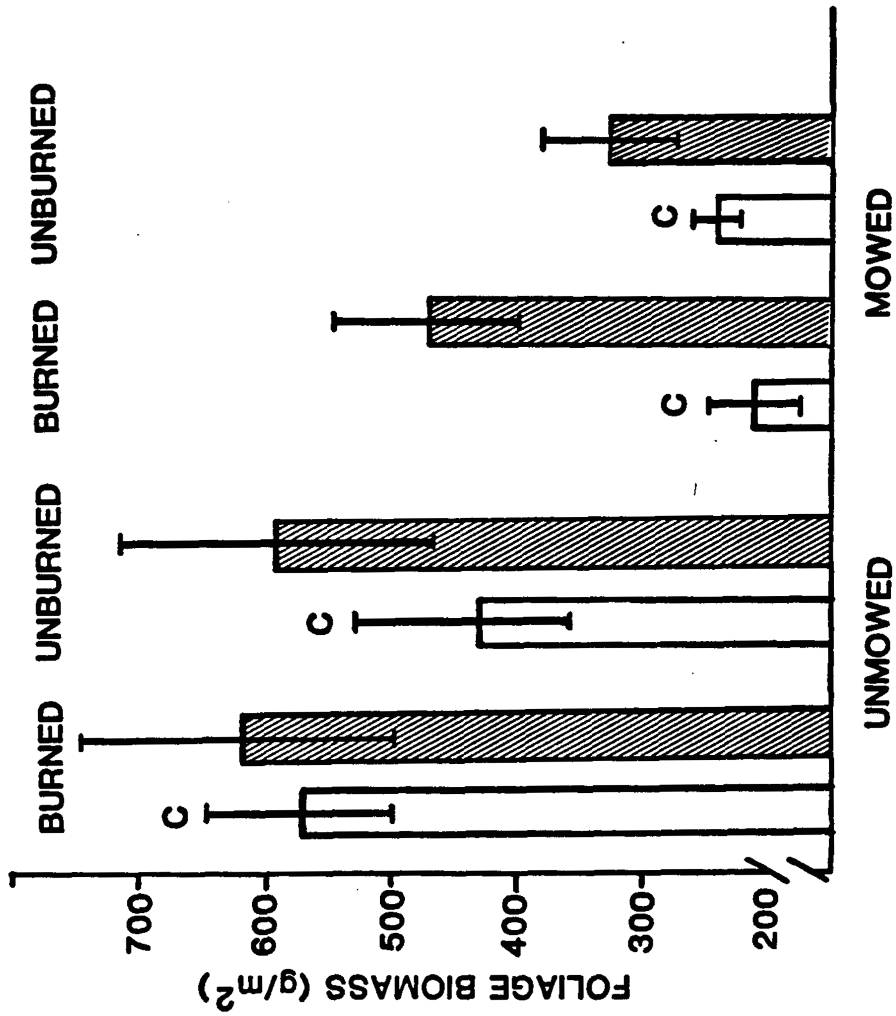
FOLIAGE BIOMASS (g/m²)
700
600
500
400
300
200
BURNED
UNBURNED
BURNED
UNBURNED
C
C
C
C
UNMOWED
MOWED

Fig 5

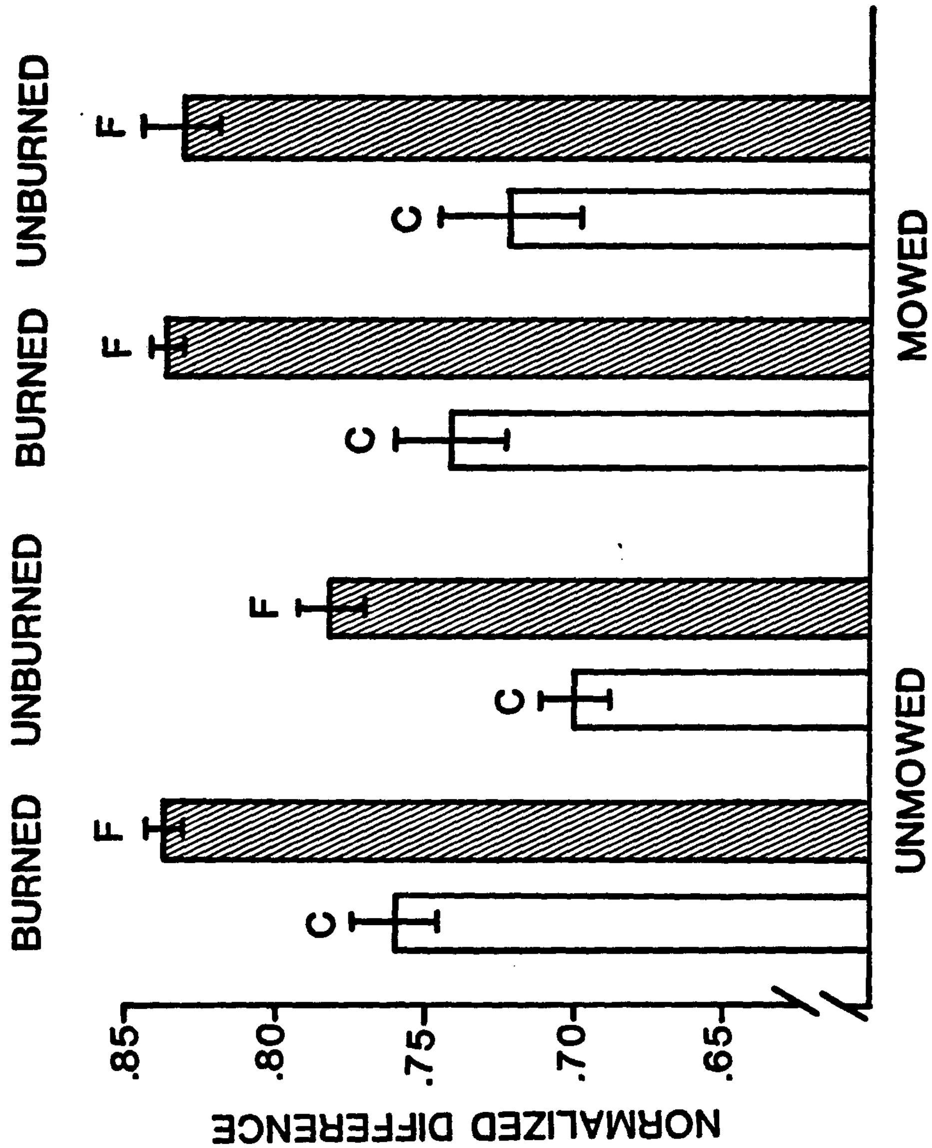
NORMALIZED DIFFERENCE
.85
.80
.75
.70
.65
BURNED
UNBURNED
BURNED
UNBURNED
C
F
C
F
C
F
C
F
UNMOWED
MOWED

Fig C

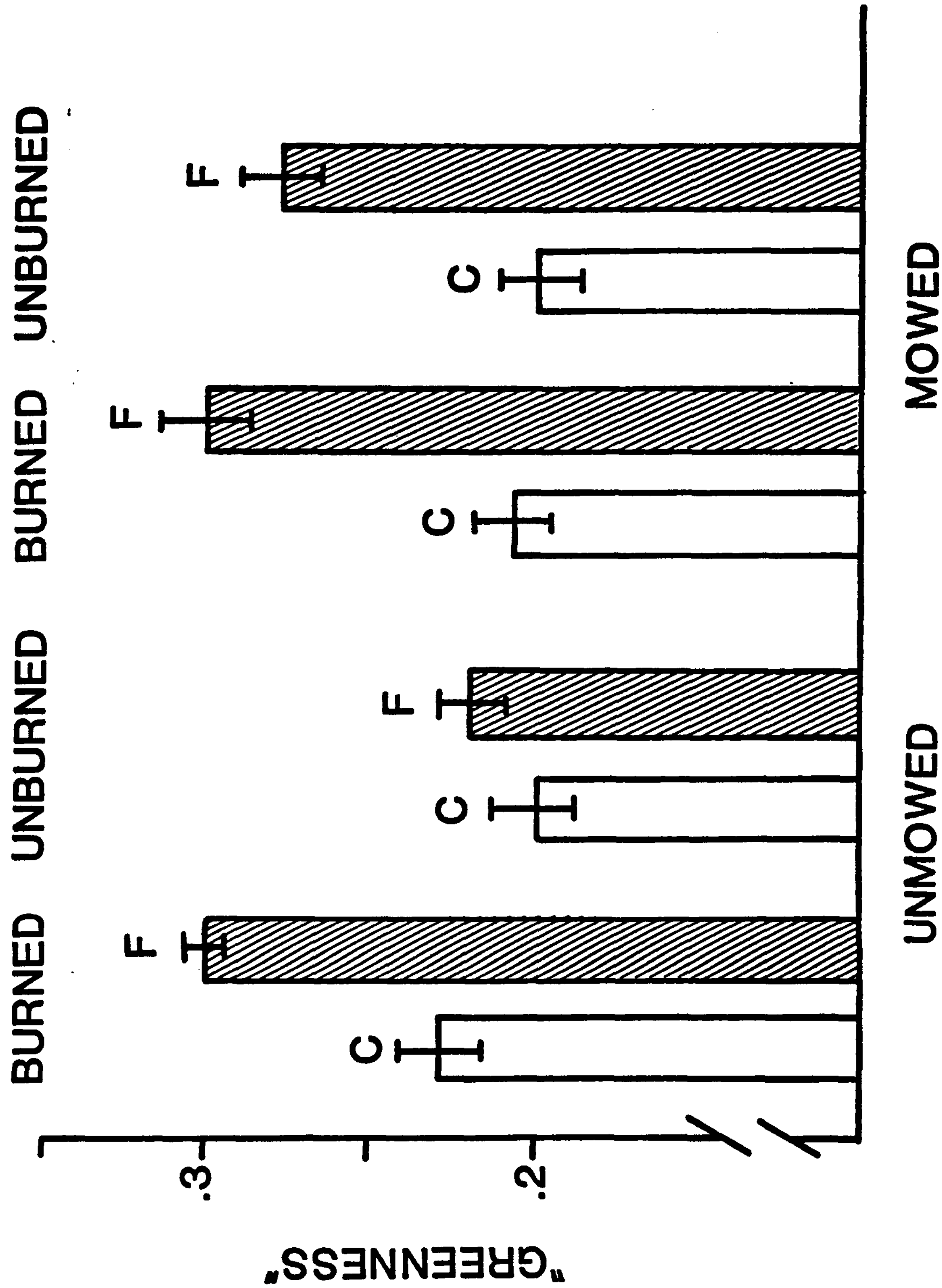
"GREENNESS"
.3
.2
BURNED
UNBURNED
BURNED
UNBURNED
C
F
C
F
C
F
C
F
UNMOWED
MOWED

Fig 7